

Descovich K, Lisle A, Johnston S, Nicolson V & Phillips C (2012) Differential responses of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*) to the presence of faeces from different species and male and female conspecifics, *Applied Animal Behaviour Science*, 138 (1-2), pp. 110-117.

This is the peer reviewed version of this article

NOTICE: this is the author's version of a work that was accepted for publication in Applied Animal Behaviour Science. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in Applied Animal Behaviour Science, [VOL 138, ISS 1-2 (2012)] DOI: <http://dx.doi.org/10.1016/j.applanim.2012.01.017>

**This is an electronic version of an article published in Vol 138 (2012) pp 110-117 in Applied Animal Behaviour Science. The article in its published form is available online at [http://www.appliedanimalbehaviour.com/article/S0168-1591\(12\)00030-5/abstract](http://www.appliedanimalbehaviour.com/article/S0168-1591(12)00030-5/abstract).*

Differential responses of captive southern hairy-nosed wombats (*Lasiorhinus latifrons*) to the presence of faeces from different species and male and female conspecifics

Descovich, Kristin A.^{ab}, Lisle, Allan. T.^a, Johnston, Stephen^{ab}, Nicolson, Vere^c & Phillips, Clive J.C^b

^aSchool of Agriculture and Food Science, University of Queensland, Gatton, QLD 4343, Australia

^bCentre for Animal Welfare and Ethics, School of Veterinary Science, University of Queensland, Gatton, QLD 4343, Australia

^cDreamworld Veterinary Clinic, Dreamworld Theme Park, Coomera 4209, Australia

Abstract

The southern hairy-nosed wombat (*Lasiorhinus latifrons*) appears to use scent marking, including defaecation, for social communication in the wild. This premise assumes that the receiver wombat is able to distinguish between faeces from different sources. To examine this theory, four types of faeces (male wombat, female wombat, dingo and a plastic control) were placed into the enclosures of 12 captive wombats. Behaviour, inter-individual distance and enclosure use were recorded during the period of placement, as well as the period before and the period after. When faeces were present, the wombats used concealed locations more often than other periods (mean %: pre-treatment: 71.3, treatment: 75.6, post-treatment: 72.7; $P < 0.05$). During the same period they also reduced grazing (mean min/period: pre- treatment: 15.8, treatment: 6.9, post- treatment: 13.1; $P = 0.0002$) and walking

activity (mean min/period: pre- treatment: 85.2, treatment: 66.9, post- treatment: 78.2; $P = 0.01$), indicating an increased perception of risk. Wombats approached the dingo faeces 5.6 times per treatment period, which was greater than for the control (3.0; $P = 0.004$) or female wombat faeces (3.7; $P = 0.049$). They also avoided other wombats most when male wombat faeces were present (8.3 retreats/period) compared to the control (4.5; $P = 0.02$), or female wombat (4.3; $P = 0.01$). There was a residual effect of increased wombat avoidance the period after presentation of dingo faeces (9.6; $P \leq 0.05$). It is concluded that the southern hairy-nosed wombat can differentiate between faeces from different species and sex of conspecifics, and that predator faeces and those from male conspecifics increase wombat avoidance behaviour either during or after presentation.

Key words

Wombat, olfactory, faeces, scent, captivity, communication

1.0 Introduction

Scent marking is an energetically efficient method of advertising position, territory and reproductive state (Brashares and Arcese, 1999). It is particularly effective when vision is restricted, such as in burrows or at night (Arakawa et al., 2008; Monclús et al., 2009). Animal odours can facilitate communication between conspecifics according to four different functions, scent matching, reproductive signaling, temporal or spatial signaling and resource protection (Begg et al., 2003). Scent matching allows a resident animal to distinguish other residents from intruders by recognizing their scent, thereby reducing the need for territorial encounters (Gosling and McKay, 1990; Le Roux et al., 2008; Luque-Larena et al., 2001). Male snow voles (*Chionomys nivalis*), for example, show less aggression and more avoidance towards males that have been recognised by scent matching than for

those without matched scents (Luque-Larena et al., 2001). This function is particularly relevant to species with overlapping boundaries, or those that operate within a hierarchical social system. Scent marks may also advertise reproductive status and receptivity as they contain gonadal steroid metabolites (Jannett, 1984; Ruibal et al., 2010; Swaisgood et al., 2000). Male captive pandas (*Ailuropoda melanoleuca*), for example, vocalise, lick, investigate and scent mark more when exposed to female faeces compared to male faeces, and they vocalise even more when the marker female is in oestrus (Swaisgood et al., 2000). When scent marks are used for reproductive purposes, behavioural differences should be evident between male and female markers and/or receivers (Begg et al., 2003), and yearly patterns should be apparent for seasonal breeders (Pal, 2003). Scent marks may repel neighbouring individuals allowing temporal and spatial relationships to be established without physical or visual contact (Begg et al., 2003; Clapperton et al., 1989; Gosling and Roberts, 2001). Free-ranging male dogs (*Canis familiaris*) mark close to boundaries shared with neighbours, while females mark closer to nesting sites (Pal, 2003), indicating that scent marks are intended to deter intruders. Scent marks around feeding sites may protect resources (Begg et al., 2003; Kruuk, 1992; Miller et al., 2003). Golden lion tamarins (*Leontopithecus rosali*) and otters (*Lutra lutra*) both mark feeding areas to reduce foraging competition. Otters also scent mark more during seasons when food is scarce (Kruuk, 1992; Miller et al., 2003).

For prey species, scent marks may provide information about predation risk (Hayes et al., 2006). Rodents (*Melomys cervinipes*, *Rattus fuscipes* and *Uromys caudimaculatus*) and cows (*Bos taurus*) avoid feeding areas where there is evidence of predators (Hayes et al., 2006; Kluever et al., 2009). Prey species may also use scent marks from co-habiting species to assess predation risk. Domestic cows exposed to deer (*Odocoileus hemionus*) scents are less vigilant and eat more, indicating a perceived reduction in predation risk (Kluever et al., 2009).

The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is an Australian terrestrial marsupial that appears to use scent marks for social and reproductive signaling (Gaughwin, 1979; Taylor, 1993). Wombats often defaecate at their burrow entrance and on conspicuous objects such as rocks (Taylor, 1993) and males have been observed to display flehmann (Gaughwin, 1979). Wombats also rub their rumps on prominent objects such as burrow entrances, although this behaviour is not influenced by gender or breeding season and may, therefore, be performed more for grooming purposes rather than for scent marking (Walker et al., 2006). Studies into the function of olfactory communication in wombats may facilitate a better understanding of reproductive and social processes in wild populations, including the critically endangered Northern hairy-nosed wombat (*Lasiorhinus krefftii*). They may also assist in the management of captive populations. To determine if southern hairy-nosed wombats use scents such as faeces for social communication or predator avoidance, it is important to determine firstly whether they can distinguish between scents from different sources and secondly how the scents from different sources affect behaviour (Swaigood et al., 2000). This study, therefore, aimed to quantify the level of differentiation and behavioural response of southern hairy-nosed wombats to faeces from conspecifics and a predator.

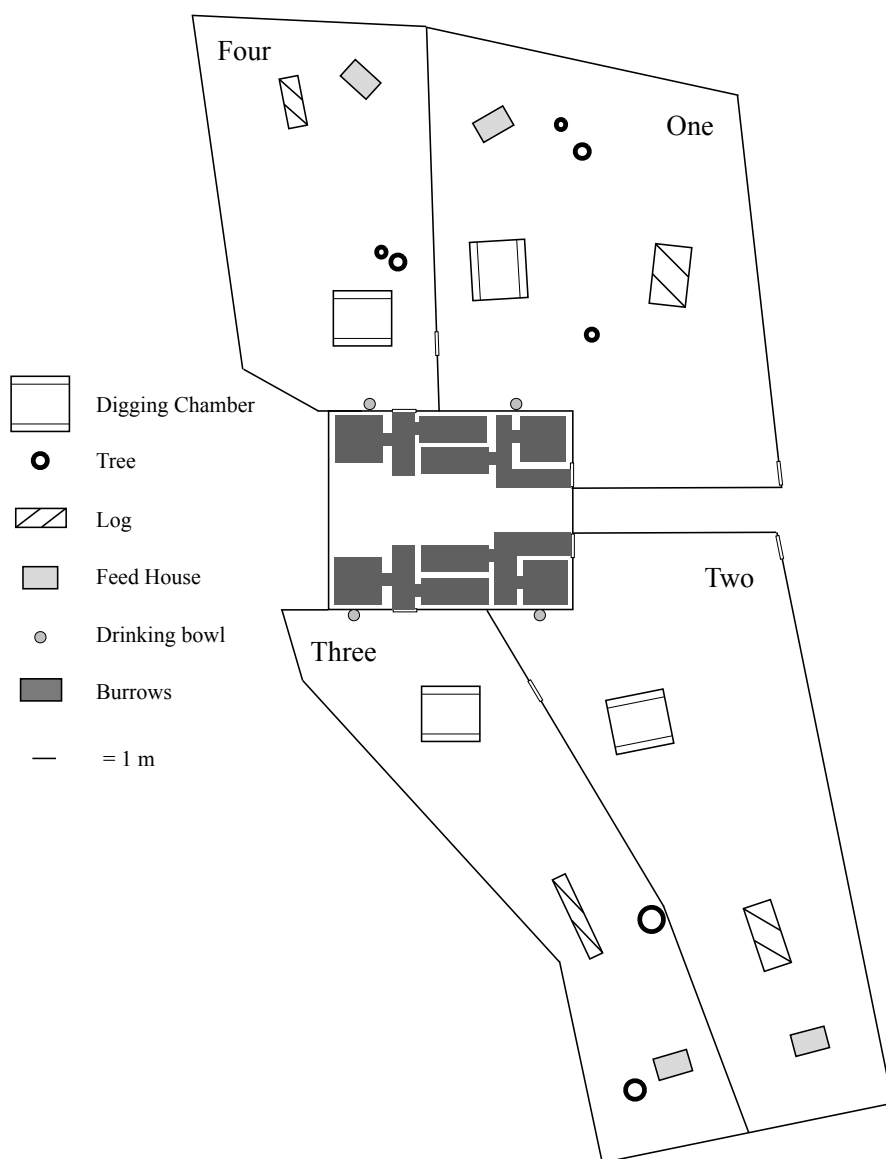
2.0 Materials and Methods

2.1 Study Animals

The study was conducted at the Rockhampton Botanic Gardens and Zoo (23° 22' S, 150° 30' E), Australia, using 12 adult southern hairy-nosed wombats housed in four groups of unrelated individuals each containing one male and two females. Eleven of these animals were wild caught prior to 2005 and the remaining one was born at the zoo in 2003. Accommodation for each wombat group was similar and included a temperature-controlled burrow system, a digging chamber, feeding house, native grass and a log (Hogan et al., 2009). The total area for each enclosure measured between 163

100 m² and 249 m² (Fig. 1). All wombats were fed carrots, chaff and macropod pellets (Riverina Australia
101 Pty Ltd., West End, Australia) daily and were weighed weekly. Each wombat wore a distinctive
102 reflective collar for identification on video. Ethics approval was obtained from the University of
103 Queensland Animal Ethics Committee (SAS/806/88).

104



105

106 *Fig. 1. Wombat enclosure design.*

107

108

2.2 Faeces treatments

Four faeces types were used as treatments in this study: natural predator, dingo (D); male wombat (MW); female wombat (FW); and control (C). The predator scats were collected on a single occasion from two adult dingoes (*Canis familiaris dingo*), one male and one female, at the Rockhampton Botanic Gardens and Zoo. After collection they were evenly mixed and distributed into four 12 g doses and frozen at -20 °C until required. Conspecific scats were collected weekly over 6 weeks from two adult *L. latifrons* wombats (one male and one female) residing at a different institution to ensure that the recipient animals were unfamiliar with the donor animals. Collection occurred outside of the breeding season and the female wombat was determined to be anoestrous from faecal progesterone metabolite concentrations (23.1, 24.8, 23.1, 24.8, 18.7, 26.9, 20.3 and 14.8 ng/g in weeks 1 – 6, analysed by the method of Hogan et al., 2010). After collection, faeces were immediately frozen at -20 °C. The MW and FW treatments were prepared by combining 2 g from each collection week for a total of 12 g per treatment. Plastic, imitation canine faeces (Dog Dirt, Loftus, Taiwan) were used as a control treatment. To avoid odour contamination, this was washed with the same detergent used to clean the wombat food bowls (Goldie, Morrison C.Q., North Rockhampton, Australia) and rinsed thoroughly with water.

Treatments were randomly assigned to the pre-established wombat groups using an orthogonal Latin square design with four rotations. All groups had access to two dens, one of which was used for sleeping. Each morning of the study the den floors were swept and faeces removed from the external enclosure. Treatment faeces were placed onto the floor of the non-sleeping den for one night from the beginning of the wombats' active phase (17:00 h) until morning husbandry (08:00 h), with an inter-treatment interval of 1 week to ensure that any previous odours had dissipated (Clark and King, 2008).

Treatments were placed directly from the sample bag without contact with human skin to avoid contamination.

2.3 Behavioural Observation

Wombat behaviour was monitored via burrow cameras (Sony Model: N11368; Ozspy, Bundall, Australia), external enclosure cameras (Sony Model: B480-312-TA; Ozspy, Bundall, Australia) and custom-made infrared (926 nm) spotlights (Hogan et al., 2009). An ethogram adapted from Hogan (2010) was used to record major behaviours at 5-min intervals and minor behaviours as counted events (Table 1). Wombats are nocturnal therefore recording periods were defined as 17:00 – 16:55 to identify effects occurring during exposure to the treatment and during the subsequent rest time, with activity recorded over three of these ‘periods’: pre-treatment, treatment, and post-treatment. To determine if faeces affected inter-individual distances or space use, the location of each wombat was recorded at 5-min intervals. Wombats in the external enclosure were allocated a grid reference location, while wombats situated inside the den system or another permanent structure, were allocated a location code (e.g. digging chamber = DC). All locations within permanent structures were categorized as ‘concealed’ locations. External locations were categorized as ‘boundary’ locations if they were ≤ 2 m from the fence line, and ‘central’ locations if they were > 2 m from the fence line.

Table 1. Ethogram of recorded major and minor behaviour for the southern hairy-nosed wombat

Major Behaviour	Description	Minor Behaviour	Description
Digging	Digging with the front paws and pushing out dirt with the back feet	Affiliative behaviour	Non-aggressive social behaviour from one wombat to another
Exploring	Investigating or examining areas of the enclosure	Approach	Approaching another wombat
Feeding	Eating of prepared food in the feeding house	Approach treatment	Approaching the treatment area by entering the secondary den
Grazing	Grazing on grassed areas or provided grass clumps	Bite	Bite from one wombat to another
Laying Rest	Resting but awake in a lying position	Body Rubbing	A body part is rubbed against an inanimate object
Mating behaviour	Mating or courtship behaviour	Drinking	Drinking of water from a provided bowl
Pacing	Repetitive pacing, usually along the enclosure boundary	Following	Non-aggressive following of one wombat to another
Sleeping	Sleeping	Object smelling	Projecting the head towards an object and smelling
Sitting Alert	Resting but awake, sitting on the haunches with front paws on the ground. Head is up in an alert position.	Retreat	Retreating from another wombat
Sitting Rest	Resting but awake, sitting on the haunches with front paws on the ground and head down.	Rolling	Rolling onto the back briefly from a standing position. May repeat or wiggle whilst on the back.
Standing	Standing on four feet, head is level with the shoulders or in a down position	Scanning	Vigilance using side to side scanning head movements
Standing Alert	Standing on four feet, head is up in an alert position	Scratching	Vigorous back and forth motion of foot claws across an area of the body
Slow Walk	A slow gait using four limbs. Primary form of locomotion	Wombat Smelling	Projecting the head towards a conspecific and smelling
Wall Climbing	Climbing action repeatedly performed at the walls in a den		

2.4 Statistical analysis

Behaviours with less than 20 (major) or 100 (minor) counts in total over the entire study were discounted from analysis, as the data were noticeably bimodal and occurred in frequencies either under or considerably over these designated thresholds. The data were analysed using SAS® (SAS Institute,

version 8.2, Lane Cove, Australia). Behavioural data were transformed (natural logarithmic transformation + one) before analysis to achieve normality of residuals, following model fitting. To determine the effects of period, sex and treatment, the transformed data were analysed using a linear mixed model with a nested design for wombat within enclosure and a repeated measures design for the periods of each treatment. Where a significant overall effect was apparent, back-transformed least square means with 95% confidence intervals were calculated and protected *t*-tests (Howell, 2010) conducted to determine if behaviour differed significantly between different periods of each treatment and between treatments within the same period. Both transformed means with standard errors and back-transformed means are reported.

Wombat location data were analysed using only data points encompassing the active phase (17:00 – 07:00 h, Hogan et al., 2011) to avoid long episodes in the same sleeping location influencing the data. Inter-individual distances were calculated from the grid references for each pair combination within a group (male - female 1; male – female 2; female 1 – female 2), unless there was a permanent structure between the animals, in which case no record was taken. Inter-individual distance and the percentage of time that pairs were separated by a permanent structure were analysed using the GLM procedure in SAS® (SAS Institute, version 8.2, Lane Cove, Australia). Enclosure use was analysed using the Genmod procedure in SAS® (SAS Institute, version 8.2, Lane Cove, Australia) with a binomial distribution with a logit link to test initially for the use of concealed locations compared to unconcealed, and subsequently, when the location was unconcealed, to test for the use of boundary locations compared to central locations. Cohen’s tests of standardized effect sizes are provided in addition to the test statistics and probability values.

3.0 Results

3.1 Behaviour

Faeces treatment significantly affected two behaviours: approach to the treatment area and retreating from conspecifics (Fig. 2). During the treatment period, the wombats approached the treatment area significantly more for treatment D compared to C ($t_{88} = 3.0$, $P = 0.004$, $d = 1.25$) or FW ($t_{88} = 2.0$, $P = 0.049$, $d = 0.84$) and retreated from conspecifics twice as often for treatment MW as for FW ($t_{88} = 2.5$, $P = 0.01$, $d = 1.18$) or C ($t_{88} = 2.3$, $P = 0.02$, $d = 1.09$). Wombats receiving treatment D increased retreating behaviour from the treatment to post-treatment period ($t_{88} = 2.11$, $P = 0.04$, $d = 0.86$), so that retreat during the post-treatment period was more frequent for D than all other treatments (D vs. C: $t_{88} = 2.8$, $P = 0.007$, $d = 1.29$; D vs. FW: $t_{88} = 2.5$, $P = 0.01$, $d = 1.16$; D vs. MW: $t_{88} = 2.0$, $P = 0.05$, $d = 0.92$). Pacing and investigatory behaviour, which are particularly important as behavioural indicators of welfare in captive animals (Carlstead et al., 1993; Mallapur and Chellam, 2002) were unaffected by treatment or period (Table 2).

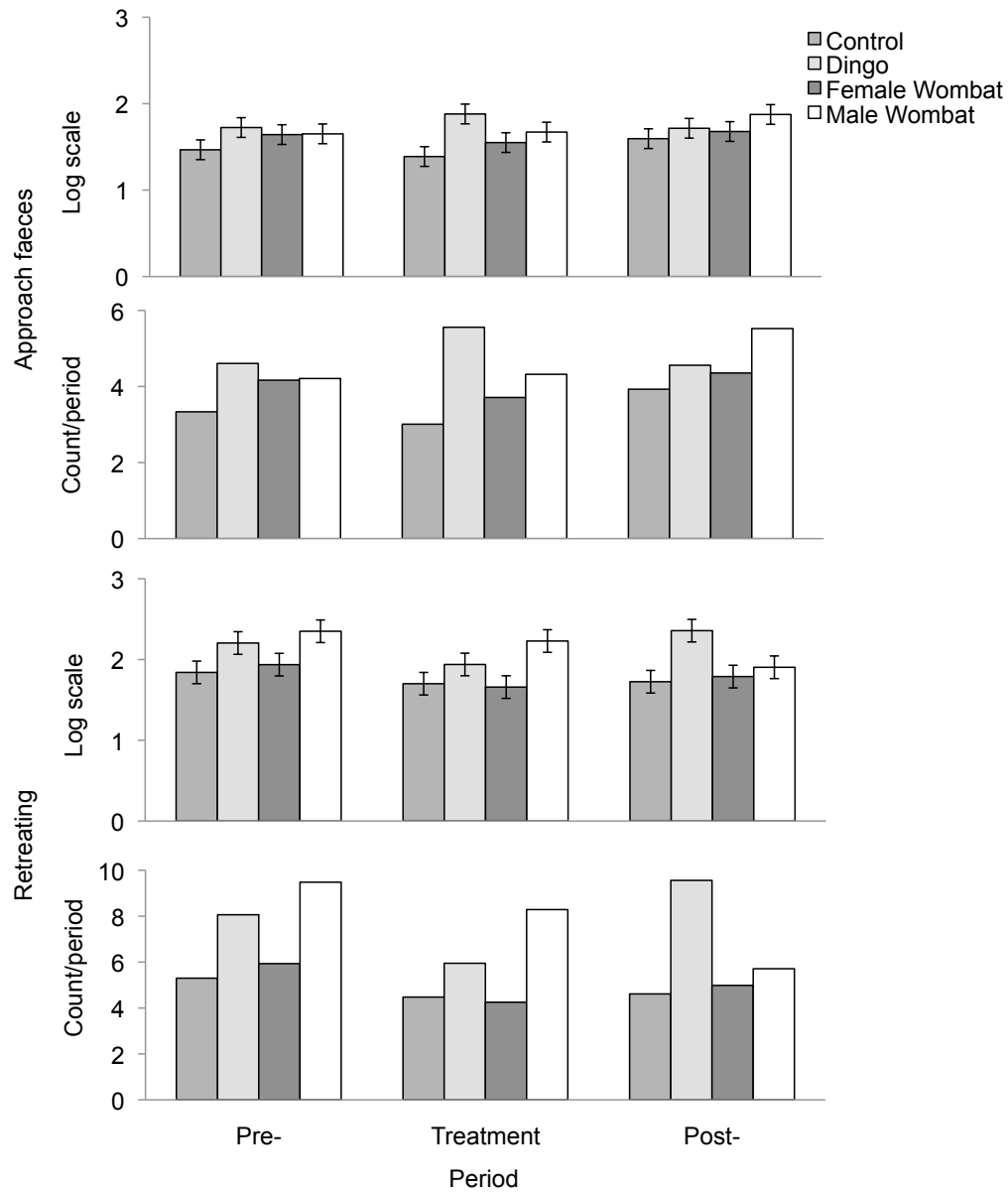


Fig. 2. The effect of faeces and period on approaching faeces treatments and retreating from conspecifics. Log transformed (natural log + 1) means with standard errors and backtransformed means are reported.

205

206 *Table 2. Pacing (min/period) and smelling behaviour (count/period)¹ in the southern hairy-nosed wombat before (Pre-), during (Treatment) and*
 207 *after (Post-) exposure to faeces. Overall F statistic and P value are given.*

208

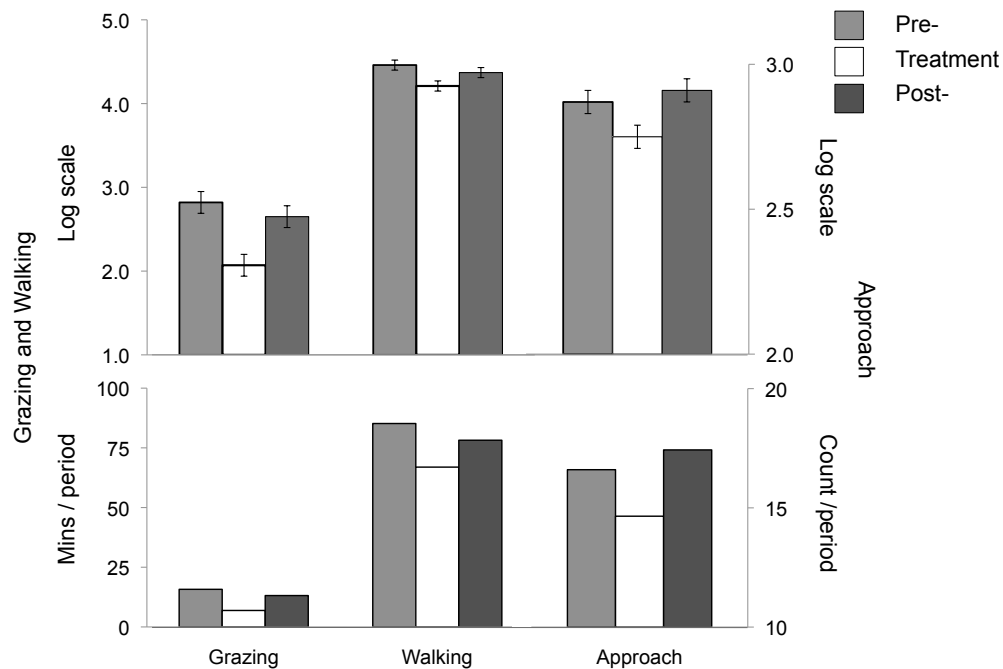
209

Behaviour	Period	Mean (Backtransformed mean; <i>d</i>)				
		Control	Dingo	Female Wombat	Male Wombat	SEM
Pacing $F_{6,88} = 0.9$, $P = 0.46$	Pre-	2.14 (7.5)	2.42 (10.3; 0.43)	2.63 (12.9; 0.75)	2.11 (7.3; -0.05)	0.19
	Treatment	2.34 (9.4)	2.03 (6.6; -0.48)	2.44 (10.4; 0.15)	1.99 (6.3; -0.54)	0.19
	Post-	2.38 (9.8)	2.14 (7.4; -0.37)	2.24 (8.4; -0.21)	2.27 (8.7; -0.17)	0.19
Smelling $F_{6,88} = 0.66$, $P = 0.68$	Pre-	2.53 (11.6)	2.38 (9.8; -0.28)	2.44 (10.5; -0.17)	2.49 (11.1; -0.08)	0.15
	Treatment	2.62 (12.7)	2.60 (12.4; -0.04)	2.67 (13.4; 0.09)	2.31 (9.0; -0.59)	0.15
	Post-	2.63 (13.0)	2.84 (16.1; 0.40)	2.61 (12.6; -0.04)	2.57 (12.1; -0.11)	0.15

210

¹ Transformed means (natural log + 1) and SEM are given. Backtransformed means and standardised effect sizes (*d*) comparing experimental to control treatments within the same period are also provided in brackets.

211
 212 Period effects were evident in three behaviours regardless of the treatment type. These were grazing
 213 ($F_{2,88} = 9.47$, $P = 0.0002$), walking ($F_{2,88} = 4.44$, $P = 0.01$), and approaching another wombat ($F_{2,88} =$
 214 3.76 , $P = 0.03$) (Fig. 3). These behaviours occurred less during the treatment period than the pre-
 215 treatment (graze: $t_{88} = 4.15$, $P = 0.0001$, $d = -0.85$; walk: $t_{88} = 2.94$, $P = 0.004$, $d = -0.60$; approach: t_{88}
 216 $= 1.91$, $P = 0.06$, $d = -0.39$) or post-treatment periods (graze: $t_{88} = 3.21$, $P = 0.002$, $d = -0.66$; walk: t_{88}
 217 $= 1.89$, $P = 0.06$, $d = -0.39$; approach: $t_{88} = 2.66$, $P = 0.009$, $d = -0.54$), although the contrasts for
 218 walking and approaching with the subsequent and previous periods, respectively, were only significant
 219 at $P = 0.06$. Male and female wombats did not differ in their response to the treatments presented in
 220 this experiment with no behaviour reaching significance for sex x treatment effects ($P > 0.05$).
 221



222
 223 *Fig. 3. Wombat behaviour (grazing, walking and approaching a group member) during pre-treatment,*
 224 *treatment and post-treatment periods. Log transformed (natural log + 1) means with standard errors*
 225 *and backtransformed means are reported.*
 226

226
227 *3.2 Inter-animal spacing and enclosure use*

228

229 Neither treatment nor period affected the distance between wombat pairs, or the frequency of
230 separation of these pairs by permanent enclosure structures (Table 3). However, wombats used
231 concealed locations more often during the treatment period (75.6 ± 1.7 % of time) compared to the
232 pre-treatment (71.3 ± 1.7 %) ($\chi^2_1 = 9.98$, $P = 0.002$) or post-treatment period (72.7 ± 1.7 %) ($\chi^2_1 =$
233 4.58 , $P = 0.03$) and this occurred irrespective of faeces type (Table 3). Patterns of use within the
234 external section of the enclosure did not change due to treatment ($\chi^2_6 = 3.89$, $P = 0.69$) or period (χ^2_1
235 $= 1.42$, $P = 0.49$) (Table 3).

236

237 Table 3. Measures of animal spacing (i and ii) and enclosure use (iii and iv)² for the southern hairy-nosed wombat before (pre-), during (treatment)
238 and after (post-) exposure to faeces.
239
240

	Period	i) Inter-individual distance (m)	ii) Occurrence of separated pairs (%)	iii) Concealed locations (logit scale)	iv) Boundary locations (logit scale)
Control	Pre-	2.9	43.8	1.13 (75.5)	0.60 (64.5)
	Treatment	2.2	42.7	1.21 (76.9)	0.60 (64.5)
	Post-	3.5	40.9	0.94 (71.8)	0.84 (69.9)
Dingo	Pre-	4.1 (1.02)	46.6 (0.71)	0.80 (68.9; -0.99)	0.56 (63.7; -0.02)
	Treatment	2.6 (0.34)	42.3 (-0.10)	1.09 (74.8; -0.31)	0.58 (64.2; -0.01)
	Post-	3.2 (-0.25)	42.6 (0.43)	0.96 (0.72; 0.04)	0.79 (68.7; -0.02)
Female Wombat	Pre-	2.7 (-0.17)	46.4 (0.66)	0.86 (70.3; -0.72)	0.52 (62.6; -0.03)
	Treatment	2.8 (0.51)	45.9 (0.81)	1.22 (77.1; 0.07)	0.55 (63.3; -0.01)
	Post-	2.0 (-1.27)	46.0 (1.3)	1.26 (7.79; 0.93)	0.41 (60.1; -0.16)
Male Wombat	Pre-	3.3 (0.34)	42.4 (-0.36)	1.07 (74.4; -0.22)	0.72 (67.3; 0.04)
	Treatment	2.5 (0.25)	41.6 (-0.28)	1.26 (76.5; 0.09)	0.74 (67.7; 0.05)
	Post-	3.2 (-0.25)	45.9 (1.27)	0.99 (72.9; 0.10)	0.74 (67.8; -0.03)
SE		0.6	2.0	0.1	0.1
Period effect		F _{2,24} = 1.53, P = 0.24	F _{2,24} = 0.78, P = 0.47	χ^2_2 = 10.40, P = 0.006	χ^2_2 = 1.42, P = 0.49
Treatment x Period Effect		F _{6,24} = 0.83, P = 0.56	F _{6,24} = 0.91, P = 0.50	χ^2_6 = 10.28, P = 0.11	χ^2_6 = 3.89, P = 0.69

² Means and SE are given, with backtransformed means (%) also provided for iii) and iv). F and P values are given for period and treatment x period effects with P < 0.05 considered significant. Standardised effect sizes (*d*) comparing experimental to control treatments within the same period are provided in brackets beside the mean for i) and ii). Approximations of the standard effect size (*d*) comparing experimental to control treatments within the same period have been calculated using data from a Mixed Model in SAS® (SAS Institute, version 8.2, Lane Cove, Australia) and are presented after the backtransformed means for iii) and iv).

4.0 Discussion

It is evident from the results of this study that wombats are able to differentiate between faeces from different species, and between sexes of conspecific donors. Studies in other herbivorous species such as Australian rodents (*Melomys cervinipes*, *Rattus fuscipes*, *Uromys caudimaculatus*) and cattle showed comparable differentiation between species (Hayes et al., 2006; Kluever et al., 2009). Giant pandas have been observed to similarly discriminate between male and female odours (Swaigood et al., 2000), although females in oestrus were not included in our study design.

The avoidance of conspecifics that occurred when male wombat faeces were presented suggests that they induced a fear of a novel and potentially aggressive male animal. Wombats have poor eyesight (Triggs, 2009) and, therefore, precautionary behaviour such as retreat from familiar animals would provide protection when a threat has been detected through olfactory communication. This suggests that an initial threat may have been perceived in response to the sight of another wombat, before confirmation could be obtained that this was a familiar group member, and not the animal that had produced the faeces. A similar process of conspecific recognition has been demonstrated in sheep (Alexander and Shillito, 1977) where initial visual and olfactory detection is followed by confirmation of identity using olfaction when sufficiently close. The avoidance of conspecifics in the period following presentation of dingo faeces suggests a delayed reaction. The dingo faeces were most often approached during the period of presentation, which may have been because of the novelty of the species information provided and the need for confirmation. It is conceivable that the wombats recognized the faeces came from a predator, which then had the residual effect of triggering a retreat response from any animals in the enclosure.

The presence of faeces did not promote exploratory behaviour of the enclosure environment or reduce the incidence of stereotypical pacing. Abnormal behaviour may occur because of under-stimulating

conditions such as small enclosure sizes (Brummer et al., 2010) or concentrated diets that reduce natural feeding behaviour (Hogan and Tribe, 2007). However, as investigatory behaviour of the environment was not increased by the presence of faeces and grazing behaviour decreased, any stimulation provided by the faeces was not sufficient to offset the time involved in abnormal behaviour. This result suggests that the use of faeces in wombat enrichment programs would be of little benefit in improving animal welfare indicators. However, as captive wombats generally exhibit poor breeding rates and high levels of stereotypical pacing, further research into the benefits of olfactory enrichment is warranted.

Large changes in behaviour occurred with the presentation of faeces regardless of the type. Hiding behaviour increased during the treatment period. Wombats are fossorial and rely on their burrow systems for protection from predators (Triggs, 2009). An increase in the use of burrows and other concealed locations in this study suggests that the wombats perceived an increased risk of threat during the treatment period, irrespective of the faeces type. Walking and grazing decreased when faeces were present and this was most likely a direct result of increased hiding behavior, as both behaviours are primarily performed in the external enclosure. This also explains why the wombats were less likely to approach each other during treatment periods compared to other periods. The control treatment in this experiment elicited the same reaction in hiding, grazing and walking behaviour as other treatments. This cannot be attributed to human interference, as the level of human presence was comparable across all periods. This suggests that either the wombats used visual information to recognize the control as faeces or responded due to neophobia because of the novelty of the stimulus. It is conceivable that the wombats used prior experience to associate the shape of the plastic control with faeces, as fox and cat scats are occasionally found in the enclosures (Descovich, pers. obs.). In dairy cows, however, research with artificial faeces has demonstrated that it is the smell and not the sight that elicits an avoidance response (Marten and Donker, 1966). The phenomenon of neophobia in response to novel stimuli is well established in captive species (Biondi et al., 2010; Fox

and Millam, 2007; Greenberg, 2003). Neophobia may also affect feeding behaviour as seen in this population, although prior studies have only measured this when the food source and novel item are in close proximity (Apfelbeck and Raess, 2008). Of the two possible explanations described, neophobia is most likely to influence the behavioural changes observed in wombats.

Inter-animal distance was unaffected by the presence or absence of the different types of faeces. Wombats in the wild are mostly solitary (Walker et al., 2007). Therefore, inter-individual distance may not accurately reflect a response to threat in this species, because unlike herding animals (Childress and Lung, 2003; Liley and Creel, 2008), wombats may not anticipate any protective advantage from close conspecific proximity.

A proposed function of social communication through faeces is for reproductive synchronization and this would be indicated when the recipient animals respond differently according to their sex. No sex differences were found in any behavioural response to faeces treatment. Potentially, this is because the influence of breeding season and oestrous cycle were controlled through the use of faeces from animals in a non-reproductive phase. Future research could include faeces sampled across different stages of the oestrous cycle and breeding season to determine the function of scats in reproductive signaling.

In conclusion, the wombats in this study were clearly able to differentiate between faeces originating from a predator, male and female conspecifics, and a plastic control. While the wombats were most affected by faeces representing the largest threats (dingo and male conspecific) all treatments triggered an increase in protective, hiding behaviour and a decrease in grazing and locomotion. This study demonstrates that faeces are an important biological signal for wombats and further study on the information gained by this species through exposure to faeces is recommended.

321

322 **Acknowledgments**

323

324 The authors would like to thank the Wombat Foundation for their financial support, and the
325 Rockhampton Regional Council and staff for animal husbandry and access to the facilities and animals
326 at the Rockhampton Botanic Gardens and Zoo. Technical advice and equipment were kindly provided
327 by Dr Alan Horsup of the Queensland Department of Environmental and Resource Management.
328 Dreamworld Theme Park supplied the Southern Hairy-nosed Wombat faeces used in this experiment.
329 The authors would also like to acknowledge the work of CQU undergraduate volunteers who kindly
330 donated their time at the Wombat Research Centre during this study, including Joel Irwin, Sarah
331 Newell, Bethlea Bell and Bec Shanks.

332

333

334 **Role of the Funding Source**

335

336 Funding for this experiment was provided by the Wombat Foundation. The funding source played no
337 role in conducting this experiment or preparing the manuscript for publication. Additionally, the
338 Wombat Foundation was not involved in the study design, or the collection, analysis and interpretation
339 of data, or in the decision to submit the paper for publication.

340

341

342

342

343 **References**

344 Alexander, G., Shillito, E.E., 1977. The importance of odour, appearance and voice in maternal
345 recognition of the young in Merino sheep (*Ovis aries*). Appl Anim Ethol. 3, 127-135.

346

347 Apfelbeck, B., Raess, M., 2008. Behavioural and hormonal effects of social isolation and neophobia in
348 a gregarious bird species, the European starling (*Sturnus vulgaris*). Horm Behav. 54, 435-441.

349

350 Arakawa, H., Blanchard, D.C., Arakawa, K., Dunlap, C., Blanchard, R.J., 2008. Scent marking
351 behavior as an odorant communication in mice. Neurosci Biobehav Rev. 32, 1236-1248.

352

353 Begg, C.M., Begg, K.S., Du Toit, J.T., Mills, M.G.L., 2003. Scent-marking behaviour of the honey
354 badger, *Mellivora capensis* (Mustelidae), in the southern Kalahari. Anim Behav. 66, 917-929.

355

356 Biondi, L.A., Bó, M.S., Vassallo, A.I., 2010. Inter-individual and age differences in exploration,
357 neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). Anim Cogn. 13,
358 701-710.

359

360 Brashares, J.S., Arcese, P., 1999. Scent marking in a territorial African antelope: The economics of
361 marking with faeces. Anim Behav. 57, 11-17.

362

363 Brummer, S.P., Gese, E.M., Shivik, J.A., 2010. The effect of enclosure type on the behavior and heart
364 rate of captive coyotes. Appl Anim Behav Sci. 125, 171-180.

365

366 Carlstead, K., Brown, J.L., Seidensticker, J., 1993. Behavioral and adrenocortical responses to
 367 environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biol.* 12, 321-331.

368

369 Childress, M.J., Lung, M.A., 2003. Predation risk, gender and the group size effects: does elk
 370 vigilance depend upon the behaviour of conspecifics? *Anim Behav.* 66, 389-398.

371

372 Clapperton, B.K., Minot, E.O., Crump, D.R., 1989. Scent lures from anal sac secretions of the ferret
 373 *Mustela furo*. *J Chem Ecol.* 15, 291-308.

374

375 Clark, F., King, A.J., 2008. A critical review of zoo-based olfactory enrichment, in: Hurst, J., Beynon,
 376 R.J., Roberts, S.C., Wyatt, T. (Eds.), *Chemical signals in vertebrates* 11, pp 391-398.

377

378 Fox, R.A., Millam, J.R., 2007. Novelty and individual differences influence neophobia in orange-
 379 winged Amazon parrots (*Amazona amazonica*). *Appl Anim Behav Sci.* 104, 107-115.

380

381 Gaughwin, M.D., 1979. Occurrence of Flehman in a Marsupial - Hairy-Nosed Wombat (*Lasiorhinus*
 382 *Latifrons*). *Anim Behav.* 27, 1063-1065.

383

384 Greenberg, R., 2003. The role of neophobia and neophilia in the development of innovative behaviour
 385 of birds. In: Reader, S.M., Laland, K.N. (eds.) *Animal Innovation*. Oxford University Press, Oxford,
 386 pp 175-196.

387

388 Gosling, L.M., McKay, H.V., 1990. Competitor assessment by scent matching: an experimental test.
 389 *Behav Ecol Sociobiol.* 26, 415-420.

390

391 Gosling, L.M., Roberts, S.C., 2001. Testing ideas about the function of scent marks in territories from
 392 spatial patterns. *Anim Behav.* 62, F7-F10.
 393
 394 Hayes, R.A., Nahrung, H.F., Wilson, J.C., 2006. The response of native Australian rodents to predator
 395 odours varies seasonally: a by-product of life history variation? *Anim Behav.* 71, 1307-1314.
 396
 397 Hogan, L., 2010. The behaviour and reproductive biology of captive southern hairy-nosed wombats
 398 (*Lasiorhinus latifrons*), PhD thesis, School of Animal Studies & School of Veterinary Science.
 399 University of Queensland.
 400
 401 Hogan, L., Phillips, C.J.C., Lisle, A., Horsup, A.B., Janssen, T., Johnston, S.D., 2009. Remote
 402 monitoring of the behaviour and activity of captive southern hairy-nosed wombats (*Lasiorhinus*
 403 *latifrons*). *Aust Mammal.* 31, 123-135.
 404
 405 Hogan, L., Tribe, A., 2007. Prevalence and cause of stereotypical behaviour in common wombats
 406 (*Vombatus ursinus*) residing in Australian zoos. *Appl Anim Behav Sci.* 105, 180-191.
 407
 408 Hogan, L.A., Phillips, C.J.C., Keeley, T., Lisle, A., Horsup, A.B., Janssen, T. & Johnston, S.D., 2010.
 409 Non-invasive methods of oestrus detection in captive southern hairy-nosed wombats (*Lasiorhinus*
 410 *latifrons*). *Anim Reprod Sci.* 119, 293-304.
 411
 412 Hogan, L.A., Johnston, S.D., Lisle, A.T., Horsup, A.B., Janssen, T. & Phillips, C.J.C., 2011. The
 413 effect of environmental variables on the activity patterns of the southern hairy-nosed wombat
 414 (*Lasiorhinus latifrons*) in captivity: onset, duration and cessation of activity. *Aust J Zool.* 59, 35-41.
 415

416 Howell, D.C., 2010. Fundamental statistics for the behavioral sciences (7th edition). Cengage Learning,
 417 Belmont, California.

418

419 Jannett, J.F.J., 1984. Scent communication in social dynamics of mammals. Acta Zool Fennica. 171,
 420 43-47.

421

422 Kluever, B.M., Howery, L.D., Breck, S.W., Bergman, D.L., 2009. Predator and heterospecific stimuli
 423 alter behaviour in cattle. Behav Processes. 81, 85-91.

424

425 Kruuk, H., 1992. Scent-marking by otters (*Lutra lutra*): signaling the use of resources. Behav Ecol. 3,
 426 133-140.

427

428 Le Roux, A., Cherry, M.I., Manser, M.B., 2008. The effects of population density and sociality on
 429 scent marking in the yellow mongoose. J Zool. 275, 33-40.

430

431 Liley, S., Creel, S., 2008. What best explains vigilance in elk: characteristics of prey, predators, or the
 432 environment? Behav Ecol. 19, 245-254.

433

434 Luque-Larena, J.J., López, P., Gosálbez, J., 2001. Scent matching modulates space use and agonistic
 435 behaviour between male snow voles, *Chionomys nivalis*. Anim Behav. 62, 1089-1095.

436

437 Mallapur, A., Chellam, R., 2002. Environmental influences on stereotypy and the activity budget of
 438 indian leopards (*Panthera pardus*) in four zoos in southern India. Zoo Biol. 21, 585-595.

439

440 Marten, G.C., Donker, J.D., 1966. Animal excrement as a factor influencing acceptability of grazed
 441 forage. Proc. Xth Int Grassld Cong, Helsinki. 359-363.

442

443 Miller, K.E., Laszlo, K., Dietz, J.M., 2003. The role of scent marking in the social communication of
444 wild golden lion tamarins. *Anim Behav.* 65, 795-803.

445

446 Monclús, R., Arroyo, M., Valencia, A., de Miguel, F.J., 2009. Red foxes (*Vulpes vulpes*) use rabbit
447 (*Oryctolagus cuniculus*) scent marks as territorial marking sites. *J Ethol.* 27, 153-156.

448

449 Pal, S.K., 2003. Urine marking by free-ranging dogs (*Canis familiaris*) in relation to sex, season, place
450 and posture. *Appl Anim Behav Sci.* 80, 45-59.

451

452 Ruibal, M., Peakall, R., Claridge, A., 2010. Socio-seasonal changes in scent-marking habits in the
453 carnivorous marsupial *Dasyurus maculatus* at communal latrines. *Aust J Zool.* 58, 317-322.

454

455 Swaisgood, R.R., Lindburg, D.G., Zhou, X., Owen, M.A., 2000. The effects of sex, reproductive
456 condition and context on discrimination of conspecific odours by giant pandas. *Anim Behav.* 60, 227-
457 237.

458

459 Taylor, R.J., 1993. Observations on the behaviour and ecology of the common wombat, *Vombatus*
460 *ursinus*, in northeast Tasmania. *Aust Mammal.* 16, 1-7.

461

462 Triggs, B., 2009. Wombats (2nd edition). CSIRO publishing, Collingwood, Victoria.

463

464 Walker, F.M., Sunnucks, P., Taylor, A.C., 2006. Genotyping of "captured" hairs reveals burrow-use
465 and ranging behavior of southern hairy-nosed wombats. *J Mammal.* 87, 690-699.

466

467 Walker, F.M., Taylor, A.C., Sunnucks, P., 2007. Does soil type drive social organization in southern
468 hairy-nosed wombats? Mol Ecol. 16, 199-208.
469
470
471
472